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LXI.—*On the Ornithosaurian Genus* Ornithocheirus, *with a Review of the Specimens from the Cambridge Greensand in the Sedgwick Museum, Cambridge.* By Reginald Walter Hooley, F.G.S.

[Plate XXII.]

The genus *Ornithocheirus* was founded by Seeley on numerous fragments of jaws and odd bones of Pterodactyls from the Cambridge Greensand, preserved in the Woodwardian (now the Sedgwick) Museum of the University of Cambridge. All the specimens are more or less water-worn. The most perfect are a humerus, femur, and several carpal bones. The first character laid down as pertaining to the genus * was "no teeth anterior to the palate," which, later †, was negatived by the statement that "the teeth are prolonged anterior to the muzzle," and another character is added, "the palate has a longitudinal ridge." In 1881 ‡ an explanation of the amendment was given, from which it appears that the genus *Ornithocheirus* was originated to include three deep club-shaped jaws of the type of *Pterodactylus simus*, Owen, and *Ptenodactylus*, for the spear-shaped jaws of the type of *Pterodactylus sedgwicki*, Owen. Hence the definition of the

* Seeley, H. G., 'Index to Aves, &c. Woodwardian Museum,' 1869, p. xvi.

† *Id.* 'Ornithosauria,' 1870, p. 112.

‡ *Id.* Geol. Mag. [2] vol. viii. 1881, pp. 15–16.

genus *Ornithocheirus* "no teeth anterior to palate"; but, becoming "convinced" that the type of *Pterodactylus simus* was a lower jaw, Seeley abandoned the genus *Ptenodactylus*, and included all the specimens under *Ornithocheirus*, being thus compelled to add the character "the teeth are prolonged anterior to the muzzle," nullifying the original character of the genus.

Further characters appear to have been added after the discovery of the toothless forms of America, when "it became evident that the bones of the skeleton are mostly formed on the same plan as those of the Cambridge genus *Ornithocheirus*." The foundation for this seems to be that portions of an edentulous jaw had been found in the Cambridge Greensand. These were determined by Owen * to be the "proximal end of metacarpal of wing," and recognized later by Seeley † as parts of the premaxillæ. In 1891 ‡ he refers to his provisional name of *Ornithostoma* for these three portions of edentulous jaws, details the resemblances to *Pteranodon*, and finds the only difference is "the American toothless Ornithosaur is twice the size." Then follows the inclusion of characters belonging to *Pteranodon* into both *Ornithocheirus* and *Ornithostoma*. The odd fragmentary bones show the same characters as the American forms, and these are made common both to the toothed and toothless. In regard to the beak, the following description reveals the confused state of things § :—"The beak varies greatly in length and in form, though it is never quite so pointed as in the American genus, for there is always a little truncation in front, when teeth are seen projecting forward from a position somewhat above the palate; the snout is often massive and sometimes club-shaped." In regard to the toothless jaw (*Ornithostoma*), it not only diverges from the original and the amended characters laid down for *Ornithocheirus* in the absence of teeth, but also "in the smooth palate formed by a single wide concave channel," which is widely at variance with the well-developed longitudinal ridge of the palate in the latter. Seeley saw evidence of the crest on specimen no. J. *c.* 8, 2, a fragment of the back of the skull which he described and figured ‖ in 1870. Twenty-one years later he still held to this, but was apparently shaken in his deter-

* R. Owen, Rep. Cret. Form. (Mon. Pal. Soc. 1859), Suppl. i. p. 18.

† H. G. Seeley, Ann. & Mag. Nat. Hist. (4) vol. vii. p. 35, footnote (1871).

‡ *Id. ibid.* (6) vol. vii. p. 441 (1891).

§ *Id.* 'Dragons of the Air,' 1901, p. 177.

‖ *Id.* 'Ornithosauria,' 1870, pl. xi. fig. 1.

mination *. An examination of this specimen shows that the bone at the junction of the parietal and occipital regions is raised into a ridge, which is continued laterally, forming the margin of the hinder border of the supratemporal fossæ. This edge is much worn, but it is clear that it was produced upwardly and outwardly, and formed no part of a backwardly directed crest. Seeley † remarks that the occiput is flat, but, if the borders were perfect, there would be a slight concavity. Above the foramen magnum are the remains of a vertical ridge. Its present vertical extent is 6 mm., its probable length in life 10 mm. Its greatest breadth is only 4 mm. It is very insignificant, and no more than the ridge along the line of the median union of the occipitals, as in many of the Reptilia. The angles at which the sides converge prove its posterior termination to have been near, with no production backwards as a crest. Seeley ‡ says "it may have given attachment to a bone like that post-superoccipital crest described by Quenstedt in the *Pterodactylus suevicus*." The surface is very small, and larger by being worn to its base, therefore no bone of any extent or strength could have been attached here. Moreover, as will shortly be shown, the crest of *Ornithostoma* (*Pteranodon*) arises superior to, overhangs, and has no connection whatever with, the occipital area. In Seeley's figure this ridge, which is depicted with too great a vertical extension, does not approach so close to the foramen magnum. The brain-case and occiput are expanded, totally unlike the compressed condition in *Ornithostoma* (*Pteranodon*), and, by its form, it suggests relationship with the toothed and pointed jaws. The sagittal crest of the genus *Ornithocheirus* is a myth. The supratemporal fossæ were apparently narrow and deep, with the parietal region of the skull constricted, as in *Ornithodesmus latidens*. No post-temporal fossæ are observable. There is nothing in the Cambridge material to prove the absence or presence of an antorbital vacuity. The facts do not favour an *Ornithostoma* (*Pteranodon*)-like skull, but one with a general form corresponding to the shrewd restoration of *Pterodactylus compressirostris* by Owen § and classified by authors under this very genus *Ornithocheirus*. The specimen J. *c.* 8, 2 was Seeley's type for the back of the skull of *Ornithocheirus*, and the only hinder region of the skull, other than J. *c.* 8, 1, known to him. It is very remarkable that all the while the Cambridge material actually

* H. G. Seeley, Ann. & Mag. Nat. Hist. (6) vol. vii. p. 443 (1891).
† *Id.* 'Ornithosauria,' 1870, p. 84.
‡ *Id. ibid.* p. 84.
§ R. Owen, Cret. Rep. (Mon. Pal. Soc. 1851) pl. xxvii. fig. 1.

included the greater portion of the hinder part of the skull of *Ornithostoma* (*Pteranodon*), from the posterior moiety of the orbits to the occiput, showing the base of a true and powerful supraoccipital crest. This interesting fossil he described and figured * as the orbito-ethmoid-sphenoid bone. The tablet J. *c.* 9, upon which this specimen is mounted, has been labelled "Ethmoid with basisphenoid." An ink-line has since been drawn through this, and someone has written "Parietal with supra-occipital." A cast in wax of the aspect shown in Seeley's fig. 9 is also on the tablet marked "cerebral hemispheres and pineal body." In pl. xi. fig. 8 * the left side is shown. As the bone is figured, the occiput is horizontal, whereas it should be oblique. The hinder border of the orbit is seen on the left upper half of the bone. The base of the supraoccipital crest extends from the top right-hand corner of the figure to the emargination near the lower. Fig. 7 * is a portion of the occiput placed upside down. The indentation in the upper border of the figure is the dorsal half of the foramen magnum, while the two foramina on either side below are the post-temporal fossæ (*cf.* Pl. XXII. fig. 2). The hinder moieties of the orbits are preserved, and are exhibited in fig. 9, pl. xi. In Seeley's explanation of the figure they are called "the cups which covered the anterior termination of the cerebral lobes." The cerebral hemispheres are not exposed at all. The frontal bone immediately posterior to the orbits is greatly compressed, becoming a deep strong keel, which intensifies in the parietal region. Here, where it meets the upper border of the occipital plane, it shows the base of a crest which is destroyed, but, from the section of the bone, it was deep and robust and produced far beyond the occiput, as in *Ornithostoma* (*Pteranodon*) (Pl. XXII. fig. 1). It has no connection with the occiput, which lies below it. The occipital area preserved is small and triangular. There is a strong median vertical ridge to the foramen magnum, on either side of which the surface is concave. In the centre of these surfaces, slightly above the level of the foramen, are the post-temporal fossæ, which are small and subcircular. The skull below the dorsal half of the foramen magnum is destroyed.

The back of the skull J. *c.* 8, 2 is the type of *Ornithocheirus*, and J. *c.* 9 belongs to *Ornithostoma* (*Pteranodon*), and the two genera are totally distinct, as the muzzles also prove. The genus *Ornithocheirus* has been given all the

* H. G. Seeley, 'Ornithosauria,' 1870, pp. 85, 86, pl. xi. figs. 7–9.

characters found amongst this medley of bones and those of the pterodactyls of the Chalk of Kansas. Its effect is seen when Professor Williston * remarks that "every essential character that has been given so far for the European species of this group agrees quite with those of our Kansas specimens. This will demonstrate how unimportant are the characters derived from the absence or presence of teeth."

In the present case the absence or presence of teeth affords a certain character, although amongst Ichthyosaurs and Aves it has been shown to be not dependable. Therefore it would be extremely unwise to follow this rule too closely, for a toothed condition is a more primitive character in this respect than a toothless. We must make use of the features we have at command when dealing with such fragmentary remains. Moreover, at the time of the deposition of the Cambridge Greensand they were an expiring race and near the end of their line, and thus we are examining the fixed or degraded characters of the ultimate descendants, and not the ancestors. Therefore the peculiarities obtaining have a greater value than if found in the beginners, for they are the specialized result of natural selection acting through ages. The situation of the front pair of teeth in some jaws, right above the palate on the anterior face of the beak, we shall shortly show is an accident caused by the wearing away of the snout. Those without teeth must for a great period have diverged from those with teeth. The fact that the seizure and prehension of food are obtained by such opposite means argues of itself corresponding variations in the form of the bones of the skull. In the Cambridge material many of the teeth are grooved and circular, and certainly more simple and less specialized than the remainder, which are more or less compressed laterally, with an absence of grooving. To conclude that the odd bones belonged to the same individuals, or even to the identical genus, as the fragments of skulls, because they happen to be found on the same horizon, is a dangerous means of diagnosis, and has not infrequently led to error in the past. This danger is intensified when we remember that the Cambridge Greensand is the remains of an old shore-line, where bones of these creatures accumulated, not only from those contemporaneous, but also probably from those derived from older beds, and could not have formed even a tithe of the flocks of these reptiles inhabiting the district.

* S. W. Williston, "Restoration of *Ornithostoma*," Kansas Quarterly, 1897, p. 35.

It appears that different families possessed the pectoral girdle characteristic of *Ornithostoma* (*Pteranodon*), e. g., *Ornithodesmus*, but the form of the skull, the position and shape of the several elements, the absence or presence, size, and position of the teeth, vary in the different genera, and are therefore the characters most to be trusted in classification. By such means the portions of skulls included in the Cambridge material under the genus *Ornithocheirus* naturally divide into five well-defined groups, and it is more than probable that they belong but to few species. The humeri and ulnæ may be arranged into three groups.

Further, Seeley * was misled by a study of the German specimens in determining the ulna as the radius and the radius as the ulna, and therefore the wrong position of these bones in the antebrachium and their place of articulation with the proximal carpal, and in stating that the radius was the larger bone.

He was studying extremely fragmentary remains, and in the German specimens the bones are so crushed that the detailed structure of their articulations is nearly indecipherable.

We shall now proceed to denote the characters by which the fragments of snouts may be classified, and give the species which naturally group themselves under each. Many of the specimens are so close to one another—which is remarkable in itself, considering their fragmentary state—that the differences in detail, which are often trivial, are of little avail until future discoveries of more complete skulls exhibit otherwise. This, we are confident from a close study of these specimens, will not be the case, and it is strange that every specimen found should have belonged to a new species. The twenty-six type-specimens in the Sedgwick Museum have been described by Seeley or Owen; therefore it will not be necessary to do that again.

Group No. 1.

Beaks laterally compressed, moderate vertical depth, tip more or less obtuse, dorsal keels. Palate curving slightly upwards anteriorly, causing the front teeth to be directed forward. Longitudinal ridge on palate, teeth subcircular, alveolar rims rising above palate.

* H. G. Seeley, 'Ornithosauria,' 1870, p. 42.

Examples :—

O. brachyrhinus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 123.
O. cuvieri (Bowerbank). Fig. J. S. Bowerbank, Proc. Zool. Soc. 1851, p. 15, pl. iv. (lettered *longirostris*); and R. Owen, Rep. Cret. Form. (1851) tab. xxviii. figs. 1–4.
O. colorhinus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 124.
O. dentatus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 119.
O. denticulatus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 122, pl. xii. figs. 8, 9.
O. enchorhynchus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 123.
O. fittoni (Owen). R. Owen, Rep. Cret. Form. (1859), Suppl. i. pl. i. figs. 3–5, and elsewhere.
O. nasutus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 120.
O. oxyrhinus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 117.
O. polyodon (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 121.
O. sedgwicki (Owen). R. Owen, Rep. Cret. Form. (1859), Suppl. i. pl. i. figs. 1, 2, and elsewhere.

These are the only specimens that truly come under Seeley's amended definition of the genus *Ornithocheirus*, viz. :—

I. Teeth prolonged anterior to muzzle.
II. Longitudinal ridge on palate.

To this group, therefore, should be assigned the generic name *Ornithocheirus*.

Group No. 2.

Beaks lanceolate and pointed, compressed laterally and vertically near the tip. Little or no upward curving of the palate. Teeth considerably smaller than in *Ornithocheirus*, uniform in size, and more or less laterally compressed. Moderate rising of alveolar rim. Longitudinal ridge on palate.

Examples :—

O. compressirostris (Owen). R. Owen, Rep. Cret. Form. (1851) pl. xxvii. fig. 5, and pl. xxviii. figs. 8, 9. 10.
O. machæorhynchus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, pl. xii. figs. 1 & 2.
O. microdon (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, pl. xii. figs. 6, 7.
O. oweni (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 115.
O. scaphorhynchus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 119.
O. tenuirostris (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 114.

We suggest that this genus be called *Lonchodectes*.

Group No. 3.

Beaks with strong lateral compression forming dorsal keel, triangular in section, truncated tip, moderate vertical depth. Dorsal outline rising from the tip at a high angle. Longitudinal ridge on palate as in *Ornithocheirus*. Very large circular teeth, anterior much larger than posterior, none directed forward.

Examples :—

O. crassidens (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 122.
O. eurygnathus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 123.
O. platysomus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 120.

To this genus we would give the name *Amblydectes*.

Group No. 4.

Massive truncated club-shaped snout, great vertical depth, longitudinal ridge on palate, teeth subcircular and vertically directed, front pair much smaller than the rest.

Examples :—

O. capito (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 126.
O. carteri (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 128.
O. platyrhinus (Seeley). H. G. Seeley, 'Ornithosauria,' 1870, p. 128.
O. simus. R. Owen, Rep. Cret. Form. (1861), Suppl. iii. pls. i. & ii., pl. iv. fig. 4.
O. woodwardi. R. Owen, Rep. Cret. Form. (1861), Suppl. iii. pl. ii. fig. 3.

For this group it would be well to give the generic name *Criorhynchus*, *Criorhynchus simus* being the type. R. Lydekker* suggested that if it "should prove generically different from *Ornithocheirus* the name *Criorhynchus* might be retained for it." R. Owen, in 1861 † and 1874 ‡, determined the type-specimen as belonging to the upper jaw, and Seeley in 1870 § remarked : "a re-examination of the type, *Pterodactylus simus*, Owen, has convinced me that it is a lower jaw." Afterwards, however (1881) ‖, he altered this view. We have a certain character to denote the upper and lower jaw in the presence of a longitudinal ridge on the palate on the former and a groove on the latter. As the ridge is to be

* R. Lydekker, B. M. Cat. 1889, p. 3.
† R. Owen, Rep. Cret. Form. (Mon. Pal. Soc. 1861), Suppl. iii. p. 2.
‡ *Id. ibid.* pt. i. (1874) p. 6.
§ H. G. Seeley, 'Ornithosauria,' 1870, p. 127.
‖ *Id.* Geol. Mag. [2] vol. viii. (1881) p. 15.

discerned*, Seeley's first decision is the correct one, which coincides with Owen's. Moreover, if this be a lower jaw, and the usual proportion of a lower to an upper obtain, the depth of the tip of the muzzle would be so excessive that the supposition becomes highly improbable.

Group No. 5.

Beak lanceolate, compressed, pointed, edentulous.
Example :—

Ornithostoma. R. Owen, Rep. Cret. Form. (1859), Suppl. i. pl. iv. figs. 4 & 5; and H. G. Seeley, Ann. & Mag. Nat. Hist. (4) vol. vii. p. 35, footnote (1871), and elsewhere.

It will be useful now to review the specimens other than in the Sedgwick Museum included by authors in the genus *Ornithocheirus,* and allot them to their particular genus, as detailed above.

Ornithocheirus clavirostris, R. Owen.

Rep. Meso. Form. (1874) pt. i. p. 6, pl. i. figs. 1–4.

Wealden (Hastings Sand), St. Leonard's-on-Sea.

In regard to this specimen Owen † was loth to believe that the "pair of teeth so anomalously located" (above the palate) was due to anything but an accident. Seeley suspected that the bone would prove to be the dentary, but the presence of the palatal ridge determines it to be the premaxillary. Neither Owen nor Seeley apparently considered the great amount of attrition to which each of the specimens had been subjected. The variation in the section of the teeth appears purely accidental, according to the degree of wear the bone has undergone. From a careful examination of the type-specimen we are confident that *Ornithocheirus* (*Coloborhynchus*) *clavirostris* is a synonym of *O. simus* and *O. woodwardi,* that they are all premaxillary bones, and that the position of the teeth, which would indeed be anomalous above the palate, is to be explained very simply: the wearing away of the tip of the snout has exposed the bases of these teeth, and not the foot of their crowns near the alveoli, as shown by the restoration (Pl. XXII. fig. 5). A similar worn condition of the sides of this specimen has displayed the bases of the teeth here also. Thus it becomes in all respects similar to *O. simus*

* R. Owen, Rep. Cret. Form. (Mon. Pal. Soc. 1861), Suppl. iii. tab. i. fig. 5.

† *Id. ibid.* (Mon. Pal. Soc. 1874) pt. i. p. 7.

(Pl. XXII. fig. 4), and therefore in future should be known as a synonym of *Criorhynchus simus*, and naturally falling into Group no. 4 as above.

Ornithocheirus daviesii (Owen).

Rep. Meso. Form. (Pal. Soc. 1874) pt. i. p. 2, pl. i. figs. 5 & 6.

The form and size of the teeth and the lanceolate shape of this dentary bone prove it to belong to Group no. 2.

Ornithocheirus giganteus (Bowerbank).

Quart. Journ. Geol. Soc. vol. ii. (1846) p. 8, pl. i., and elsewhere.

The tip of the muzzle of both the upper and lower jaw.

We are convinced that its conical shape has been produced by vertical expansion due to pressure, and possibly its width proceeds from the same cause. Taking this into consideration, and also the type of the teeth, which are strongly characteristic, this species can be included within Group no. 2.

Ornithocheirus reedi (Seeley).

Geol. Mag. [2] vol. viii. (1881) p. 13, pl. i. fig. 3.

Seeley* says this species "closely resembles *Ornithocheirus capito*"; therefore it comes into Group no. 4.

Ornithocheirus sagittirostris (Owen).

Rep. Meso. Form. (Mon. Pal. Soc. 1874) pt. i. p. 3, pl. ii.

These mandibular rami from the Wealden, by the angle of their convergence towards the symphysis, and the form, size, and arrangement of the teeth belong to Group no. 2.

Ornithocheirus xyphorhynchus (Seeley).

'Ornithosauria,' p. 117; and Geol. Mag. [2] vol. viii. (1881) p. 18, pl. i. fig. 2.

In the former paper Seeley determined this fragment to be a part of a premaxillary, in the latter of a dentary. It is very close to *Ornithocheirus sedgwicki*, and should therefore be included in Group no. 1.

* H. G. Seeley, 'Ornithosauria,' 1870, p. 127.

Ornithocheirus clifti (Mantell). Portions of humerus.

'Medals of Creation,' vol. ii. (1844) p. 806, woodcut 149.

Ornithocheirus curtus (Owen). Distal end of tibia.

Rep. Lias Form. (Mon. Pal. Soc. 1870) pt. ii. p. 52, pl. xix. figs. 8, 9.

Ornithocheirus diomedius (Owen). Distal end of ulnar metacarpal.

Brit. Foss. Mam. and Birds (1846), p. 545, woodcut 230.

Ornithocheirus nobilis (Owen). Portion of wing-phalange, ? ulna.

Rep. Lias Form. (Mon. Pal. Soc. 1870) pt. ii. descr. to pl. xix. fig. 10.

These species, founded on fragments of bones, must for the present remain in the genus *Ornithocheirus*, but for no other reason than that they have been placed there, for the characters of the bones belonging to the genus *Ornithocheirus* are absolutely unknown.

The Vertebral Column.

In regard to the bones of the vertebral column, there is not much in the Cambridge Greensand specimens, by reason of their fragmentary and worn condition and their non-association with parts known to belong to given species, to help one in classification. Some of the cervicals are fairly perfect. Seeley * denotes two groups :—

(I.) Narrow neural arch with high neural spine, pneumatic foramen oblique. Ventral face of centrum oblong and flattened.

He gives as example that figured by Owen † as belonging to *Pterodactylus simus*.

(II.) Wide neural arch, pneumatic foramen horizontal. Side of centrum makes a right angle with the base (p. 68). Ventral surface convex.

Example given, *Pterodactylus simus* (Owen) ‡.

* H. G. Seeley, 'Ornithosauria,' 1870, p. 66.

† R. Owen, Rep. Cret. Form. (Mon. Pal. Soc. 1861), Suppl. iii. pl. ii. fig. 4.

‡ *Id. ibid.* (Mon. Pal. Soc. 1859), Suppl. i. pl. ii. fig. 1.

Dorsal Vertebræ.

Seeley * classifies these vertebræ into two groups by the same characteristics. He gives as examples those figured by Owen † in his memoir on *Pterodactylus sedgwicki*. There is no justification for Owen assigning either the cervical to *P. simus* or the dorsal to *P. sedgwicki*, nor for Seeley the flat cervicals to *Ornithocheirus*. The characters pertaining to any particular genus cannot yet be definitely given.

The Notarium.

Bones which in Ornithosauria were included in the sacrum and the os innominatum, and numbered and figured respectively

J. *c.* 4, 1.	Ornithosauria.	Pl. x.	Figs. 8, 9.
J. *b.* 10, 3.	do.	Pl. viii.	Fig. 3.

by the discovery of the blending of the early dorsal vertebræ into the so-called notarium of the American form *Pteranodon*, were found to belong to this portion of the axial skeleton. Owen ‡ described and figured a bone from the Cambridge Greensand which belongs to the notarium as "probably frontal." The specimen J. *c.* 4, 1 was figured in the restoration of the pectoral girdle by Seeley in 1891 § and 1901 ‖. Both of these differ in detail from the original vertebra which is figured in Ornithosauria. Prof. Williston ¶ has pointed out that the vertebra of these figures is "undoubtedly wrong."

It would, perhaps, be safe to assign to *Ornithostoma* all the specimens belonging to the notarium, because we have the American evidence of its obtaining in *Ornithostoma* (*Pteranodon*), while there is none as regards the dentigerous jaws from Cambridge.

The Sacrum.

The six specimens of sacral vertebræ are so destroyed that it is impossible to say whether the transverse ribs were anchylosed at their distal extremities as in *Ornithostoma* (*Pteranodon*). Nos. 1 and 2 have the ventral surface of the

* H. G. Seeley, 'Ornithosauria,' 1870, p. 69.

† R. Owen, Rep. Cret. Form. (Mon. Pal. Soc. 1859), Suppl. i. pl. ii. figs. 20 & 23, and figs. 24 & 25.

‡ *Id. ibid.* p. 12, pl. iv. figs. 6–8.

§ H. G. Seeley, Ann. & Mag. Nat. Hist. (6) vol. vii. p. 411, fig. 2 (1891).

‖ *Id.* 'Dragons of the Air,' 1901, p. 115.

¶ S. W. Williston, Kansas Univ. Quart. 1897, p. 14.

centrums flat and 3 to 7 convex. In specimen J. *c.* 4, 3, which consists of three vertebræ, the bases of two transverse ribs are preserved.

The Caudal Vertebræ.

The examples determined as caudal vertebræ by Seeley in 'Ornithosauria' he later* believed to be cervicals. Some are doubtless centrums of cervicals. The absence of transverse processes and their amphiplatyan nature bring them close to *Ornithostoma* (*Pteranodon*).

The Scapula and Coracoid.

These bones may be separated into two groups. One of these, typified by specimens J. *a.* 3, was figured by Owen †. This example is very interesting, because it exhibits on the inner side of the scapular arch the bar of bone bracing the scapula and coracoid, and enclosing a foramen similar to that mentioned by Prof. Williston ‡ as found in *Ornithostoma* (*Pteranodon*) and *Nyctosaurus*. There would not seem to be further proof required that this type of scapula-coracoid belongs to the toothless English genus *Ornithostoma*. The coraco-scapular suture is oblique to the long axis of the glenoid cavity. The head of the coracoid is not so globular as that typified by J. *c.* 4, 18, 6. This specimen, figured by Seeley §, is characterized by the absence of the bar of bone, interior to the anchylosed humeral extremities of these bones. Both these two types are easily differentiated from *Ornithodesmus latidens* by the diagonal direction of the line of anchylosis of the scapula with the coracoid across the glenoid articulation, which in the latter is horizontal. The type, J. *c.* 4, 18, 6, is very nearly similar in form to the latter, and both are alike in the non-presence of the inner bar of bone.

The Humerus.

Seeley ‖ mentions fifty specimens of this bone. J. *a.* 8, 1 may be dismissed as useless. It is part of a large limb-bone, from its size more probably Dinosaurian, for it is

* H. G. Seeley, Quart. Journ. Geol. Soc. 1875.

† R. Owen, Cret. Form. Rep. (Mon. Pal. Soc. 1859), Suppl. i. p. 111, fig. 1.

‡ S. W. Williston, Kansas Univ. Quart. 1897, p. 43; and Field Col. Mus. Pub. 78, geo. ser. vol. iii. no. 3, pp. 140–141.

§ H. G. Seeley, 'Ornithosauria,' 1870, pl. i. fig. 10.

‖ *Id. ibid.* p. 38.

Proximal Ends of Humeri.

Group A.	Group B.	Group C.
1. Deltoid crest strongly developed, set at right angles to the long axis of proximal condyle, with the lower half of its distal extremity directed towards the shaft of the bone.	1. Deltoid crest not preserved; it had its origin further down the shaft than either Group A or C, and apparently slightly oblique to the long axis of the proximal condyle.	1. Deltoid crest strongly developed and produced obliquely to the long axis of the proximal condyle. No curve of distal extremity to the shaft.
2. Ulnar crest moderately developed.	2. Ulnar crest strongly developed.	2. Ulnar crest strongly developed.
3. Pneumatic foramen under ulnar crest, dorsal surface, near the articulation.	3. Pneumatic foramen under ulnar crest, dorsal surface, further from articulation than Group A.	3. Pneumatic foramen on the ventral surface, situated medianly, very near the articulation.
4. Proximal condyle strongly arched over dorsal surface.	4. Proximal condyle feebly arched over dorsal surface.	4. Proximal condyle moderately arched over dorsal surface.
5. Articular surface of condyle perfectly smooth, no ridge present.	5. Articular surface of condyle with transverse ridge, preaxial side.	5. Articular surface of condyle smooth, no ridge present.
6. Proximal condyle very crescentic.	6. Proximal condyle feebly crescentic, horns splaying outwards.	6. Proximal condyle moderately crescentic.
7. Proximal ventral surface of shaft very concave.	7. Proximal ventral surface flat.	7. Proximal ventral surface feebly concave.
Examples: nos. 14, 25, 26.	Examples: nos. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18, 19.	Examples: nos. 22, 23, 24, 27, 28, 30.
Type, J. *a.* 6, 25.		Type, J. *a.* 6, 30.

Distal Ends of Humeri.

Group A.	Group B.	Group C.
1. Condyle, preaxial side, dorsal half slightly convex for the ulna, on the ventral half a weak trochlea for the radius. No median convexity.	1. Condyle preaxial side, with two nearly flat oblique surfaces, the dorsal for the ulna looking distally, the ventral for the radius looking ventrally.	1. A preaxial and median convex condyle, a concavity between them forming a true trochlea for the ulna. An articular facet for radius on the inner surfaces of the horns of the crescentic distal end.
2. Circular opening into bone.	2. Circular opening into bone.	2. No opening into the bone.
3. Articular facet as seen in Groups B and C not present.	3. Concave oval articular facet, postaxial side, slightly oblique.	3. Concave oval articular facet, postaxial side, looking outwards.
4. Ulnar tubercle very robust, entirely on preaxial border.	4. Ulnar tubercle very robust, entirely on ventral border.	4. Ulnar tubercle weak, entirely on ventral border.
5. Two ridges, one on preaxial, the other on postaxial, border of ventral surface of shaft.	5. As in Group A.	5. Ridge on preaxial border of ventral surface of the shaft only.
6. Deep transverse valley from ulnar tubercle to central opening into the shaft.	6. Absent.	6. Absent.
Examples: nos. 21, 31, 32.	Examples: nos. 20, 29, 33, 34, 35.	Examples: nos. 30, 36, 37, 42, 43, 44, 45, 46.

apparently from the central area of the shaft, where the bone is smallest in Pterodactyls. The complete bone would therefore be of enormous bulk, and, with the other bones of the skeleton in proportion, we should have a reptile too heavy for flight. Moreover, it reveals no constriction as seen in the Pterodactyl humerus. Whether we take the proximal or distal ends, the forty-nine specimens naturally form three groups. In one group the entire bone is known for certain by the perfect example J. *a.* 6, 30, and by comparison with *Ornithodesmus latidens* another is nearly as sure, and there is reason to believe that the third group is comprised of those proximal ends which are different from the other two groups, although there can be no positive determination until a perfect humerus with the same characters is discovered. We give on pp. 542–543 the characters of the three groups and their examples, and follow by a criticism of some of the specimens included in the groups :—

Proximal ends.

Group A.

Seeley * gives J. *a.* 6, 25 as an example of the same kind of proximal end as seen in the perfect humerus, J. *a.* 6, 30, "having the pneumatic foramen radially situated on the anterior aspect near the articular surface." The pneumatic foramen is, however, found on the postaxial side posterior surface as a small circular hole in an oval-shaped depression. On its distal margin it is worn away, but the foramen can be well determined. In J. *a.* 6, 30 the deltoid crest is produced obliquely to the long axis of the condyle, while in J. *a.* 6, 25 it is nearly a right angle with little or no curve until its termination contiguous to the preaxial border of the shaft. In J. *a.* 6, 25 the outer surface of the deltoid crest is flat. As the crescent-shaped condyle in this specimen has a greater curve than that of the other examples in this or the remaining groups, a greater convexity is found on the dorsal and a greater concavity on the ventral margin. J. *a.* 6, 26 approaches closely in character to J. *a.* 6, 25 ; but, although the crest is carried as far down the shaft as in that specimen, it is produced more obliquely to the long axis of the condyle, recalling J. *a.* 6, 30 (Group C) in that respect only.

* 'Ornithosauria,' 1870, p. 39.

Group B.

J. *a.* 6, 4. Proximal end of right humerus. The deltoid crest has its origin far below the condyle, and is apparently slightly oblique to its long axis. The pneumatic foramen is further down the shaft than in J. *a.* 6, 26 (Group A), and there is a ridge on the preaxial moiety of the condyle. The condyle is not so crescentic, and therefore the horns splay more outwards and the ulnar crest is moderately developed.

Group C.

The perfect humerus J. *a.* 6, 30, whose characters have been given by Seeley, is the type. J. *a.* 6, 22, 23, 24. 27, 28 are proximal ends exhibiting pneumatic foraminæ on the ventral surface, and 38, 39, 40, 41 should also apparently have been included, although they are too much abraded to reveal the pneumatic foramen.

Distal ends.

Group A.

J. *a.* 6, 21 & 32. Examples belonging to left humeri. They are similar to *Ornithodesmus latidens*, though one-fifth smaller in the transverse diameter of the distal articulation, and the characters are very weakly developed. The central circular cavity and the transverse valley in no. 32 are filled with phosphate of lime, and thus are not well seen, while in No. 31 these are obscured by the bone being much worn in this region and destroyed on the dorsal margin of the median pit. The ulnar articulation on each bone is also worn, and does not appear to have been as highly developed as in *Ornithodesmus latidens*. Seeley says* that the "mesial condyle in this group appears in every case to be an epiphysis which is wanting." The narrow ridge on the proximal end of the ulna requires a valley to articulate in, and this would be impossible if a mesial condyle had been present.

J. *a.* 6, 31. This example possesses the same characters as nos. 21 and 32, although in a very incipient stage. It is interesting because the central circular entrance into the bone is not present. In that region occurs a basin-shaped hollow only.

* H. G. Seeley, 'Ornithosauria,' 1870, p. 40.

Group B.

J. *a.* 6, 35. This example was figured by Owen * and also by Seeley †. It differs from *Ornithodesmus latidens* in the circular pit on the articular surface being postaxial, while in the Atherfield specimen it is nearer the preaxial. The preaxial or radial area of the Cambridge specimens, as described by Owen ‡, "shows a slightly convex surface occupying its major part, and a small well-defined flat surface placed obliquely." The "slightly convex surface" becomes more convex ventrally as it nears the flat oblique surface. With a part of the former and the whole of the latter the radius articulated; but the dorsal moiety of the "slightly convex surface" was a portion of the ulnar articulation, which is continued round the dorsal margin to the postaxial edge (ulnar side), where it becomes an oval concave surface. The ulnar tubercle is placed on the ventral border only, and not on the postaxial, as in *Ornithodesmus latidens*. By nos. 20, 29, 33, and 34 it is seen that in this group there is no transverse valley, but that the ulna apparently occupied the whole of the transverse diameter of the articular end.

Group C.

The most perfect distal end of this group is J. *a.* 6, 36. It is crescentic, with the convexity on the dorsal side. The articulation exhibits a radial and median convexity, with a depression between them, forming a trochlea. On the ventral margin of the postaxial side there is a tubercle directed distally, and dorsal to this an oval concave facet, obliquely placed and looking outwards. On the ventral surface, between the horns of the crescent, there is a deep concavity, and, as the radial and ulnar condyle both have a flat facet looking inwards, it is probable that the radius articulated with both these.

The type of ulna shown on tablet J. *a.* 9, no. 1, we believe to belong to this group, because of its similar articular surfaces.

It is highly probable that the proximal ends of Groups A,

* R. Owen, Rep. Cret. Form. (Mon. Pal. Soc. 1851), Suppl. i. pl. iv. figs. 1–3.

† H. G. Seeley, 'Ornithosauria,' 1870, pl. iv. fig. 14.

‡ R. Owen, *loc. cit.* p. 16.

B, C will be found to belong to the distal ends of Groups A, B, C as now classified. That Group A belongs to a genus of the family Ornithodesmidæ appears to be certain by a comparison with the humerus of *Ornithodesmus latidens*, and from Prof. Williston's* description of the distal end of the humerus of *Ornithostoma* (*Pteranodon*) we consider the distal ends of Group B to belong to that genus, and therefore to the edentulous forms of the Cambridge Greensand. Whether the proximal ends of this group are rightly apportioned is a more difficult matter to determine, for the base is all that remains of the deltoid crest, the most characteristic feature. On examination of these specimens it appears that it was oblique to the long axis of the condyle, which, as far as it goes, agrees with Prof. Williston's† description of the crest in *Ornithostoma* (*Pteranodon*). "This process, the radial or deltoid, has its convex rounded extremity directed obliquely forward and upward and outward," yet at the same time it resembles, perhaps in a greater degree, his account of *Nyctosaurus* ‡, "the deltoid, radial, or lateral process very large." "It is directed forward and a little downward." He also says, "The ulnar or median process is very stout." This, together with the fact that the crest is more distal to the condyle in *Nyctosaurus*, seems to favour a greater affinity to *Nyctosaurus* than to the proximal ends in Group B (*? Ornithostoma*). Thus, he remarks §, "This crest is further removed from the head of the bone than is the case in species of *Pteranodon*." Perhaps with the details now given for this group an examination of the American specimens would enable a decision. At any rate, they do not belong to Groups A or C, and thus in all probability pertain to the edentulous forms. In regard to Group C, typified by the perfect humerus J. *a.* 6, 30, there is not even a suggestion to be obtained from known facts as to which, if any, of the remaining genera, formed on the evidence of the premaxillæ, it belongs.

Radius and Ulna.

The specimens on tablet J. *a.* 9 are the proximal ends of

* S. W. Williston, "Restoration of *Ornithostoma*," Kansas Univ. Quart. 1897, p. 45.

† S. W. Williston, *ibid.* p. 44.

‡ *Id.* Field Col. Mus. Pub. 78, geo. ser. vol. ii. no. 3, p. 141.

§ *Id.* Kansas Univ. Quart. vol. i. 1892–3, p. 6.

ulnæ. Corrections must be made on all the other tablets, as well as in the letterpress and figures of 'Ornithosauria':—

Tablets.

J. *a.* 10*. Distal ends of ulnæ, *not* "radii."
J. *a.* 11. Proximal ends of ulnæ, *not* "radii."
J. *a.* 12. Distal ends of radii, *not* "ulnæ."
J. *a.* 13. Proximal ends of radii, *not* "ulnæ."

Letterpress and titles, 'Ornithosauria.'

P. 43, *for* I. Distal end of "Ulna," *read* Radius.
P. 44, "Nos. 5 and 6 on another tablet (? tablet J. *a.* 13) appear to be distal ends of ulna." *For* "ulna" *read* radius.
P. 44, *for* II. Distal End of "Radius," *read* Ulna.
P. 46, *for* IV. Proximal End of "Radius," *read* Ulna.

Figures.

Plate II. Figs. 7, 8, & 9. Proximal ends of right ulna, *not* "radius."
Plate III. Fig. 1. Ventral view of distal end of left ulna, *not* "radius."
Fig. 2. Dorsal view of distal end of left ulna, *not* "right radius."
Fig. 3. Distal articulation of left ulna, *not* "right radius."
Fig. 10. Distal end of right radius, *not* "ulna."
Fig. 12. Distal end of left radius, *not* "ulna."
Plate XI. Fig. 7. Specimen J. *c.* 9, *for* "palatal aspect of the basisphenoid bone" *read* "upper portion of occiput"; the figure is upside down.
Fig. 8. Specimen J. *c.* 9, *for* "ethmo-sphenoid mass" *read* left lateral view of posterior moiety of skull of *Ornithostoma*.
Fig. 9. Specimen J. *c.* 9, *for* "posterior aspect of same specimen" *read* "anterior aspect"; the "cups" are the posterior boundaries of the orbits.

Radius.

There are only three specimens of the proximal end of the radius and four of the distal, and these are so close in characters that they may be included in one group.

Proximal end.

1. Dorsal surface convex, ventral concave.
2. Preaxial border produced outwards and forwards, the postaxial straight.
3. Articular surface, preaxial side, convex looking outwards; postaxial concave looking proximally.
4. Moderately compressed dorso-ventrally, width pre-postaxially apparently maintained down the shaft.

* There are eleven examples on this tablet, the eleventh perhaps attached since 'Ornithosauria' was written.

Distal end.

1. Dorsal and ventral surface slightly convex.
2. Articular surface a convex roll, compressed more or less dorso-ventrally, in the median area.
3. Preaxial border flat.

In regard to the proximal extremities affixed to tablet J. *a.* 13 *, specimens 5 and 6 belong to the same species as far as can be ascertained. No. 6 is not well preserved. An unnumbered specimen is near to 5 and 6, with the articular features less prominent. The main difference between these bones and those of *Ornithodesmus latidens* lies in the latter being flatter and rapidly lessening in size down the shaft. The former are stouter and reveal little or no decrease distally. Between the two surfaces of the articular end of *Ornithodesmus latidens* there is a transverse ridge across the short diameter of the bone, which fits into the valley between the two condyles of the trochlea of the humerus. This is not seen in the Cambridge specimens; therefore they probably do not belong to distal ends of the humeri J. *a.* 6, 21 and 32, Group A, where a feeble incipient trochlea is to be observed, but to Group B.

Of the four specimens of the distal ends of the radius, J. *a.* 12, 1–4, not one belongs to the same genus as *Ornithodesmus latidens*, for, although there is a general similarity in form, they differ in details. The dorsal and ventral surfaces of *Ornithodesmus latidens* are flatter and more compressed than any of the Cambridge specimens. The ventral surfaces of nos. 1 and 3 are more concave. In all four specimens, including *O. latidens*, the articular surface is a complete convexity from the pre- to the postaxial border, and all exhibit more or less constriction of this convexity on both dorsal and ventral borders in the median region. Nos. 1 and 3 belong to the same species. The preaxial border is not flattened in *O. latidens* as in the Cambridge specimens, but is robust and convex. The bone is much more concave near the articulation on the ventral surface, preaxial side. There is a longitudinal groove for muscle-attachment, contiguous with the postaxial border on the ventral surface, which is not seen in the Cambridge specimens. In *O. latidens* on the postaxial side of the dorsal surface there is a well-developed ridge and striæ, caused by the fibres of the muscles traversing the bone

* There is an unnumbered specimen on this tablet.

diagonally from the preaxial distal border. This is not exhibited in the Cambridge examples. The specimen no. 2 is not as compressed as nos. 1 and 3, or as *Ornithodesmus latidens*, and the dorsal surface is more concave distally.

The Ulna.

Proximal end.

The six specimens on tablet J. *a.* 9 are the proximal ends of ulnæ. Nos. 1, 2, 4, and 5 are figured in 'Ornithosauria,' plate iii. figs. 4, 5, 6, 7, 8, 9. J. *a.* 9, 1, belonging to the left ulna, differs from *Ornithodesmus latidens* in the absence of the longitudinal ridge on the ventral surface of the shaft, in lieu of which there is a raised and roughened surface, preaxial to the radius instead of postaxial, for the attachment of the biceps tendon. This feature is also seen in nos. 2 and 4. The dorsal surface is strongly convex, and the ventral slightly, and free from any pit or ridge. The pneumatic foramen is near the articulation in the centre of the ventral surface. The articulation is much worn. This specimen is interesting, because from it Seeley obtained the suggestion of an olecranon *. There is a well-defined line around the upper dorsal half, which might be accidental. The surfaces in all the other examples appear to be articulatory, and the roughened edges the effect of wear, and not caused by the tearing away of an epiphysis. The main articulatory surface is an oblique oval-shaped basin, looking upwards, in the centre of which in specimens nos. 4, 5, and 6 is a circular opening into the shaft, as is seen in the humerus of *Ornithodesmus latidens* and in J. *a.* 6, nos. 20, 21, and 32. Moreover, the general form of the bone is not very different from the distal extremities of the humeri, exhibiting the circular opening into the shaft—for example, J. *a.* 6, 20. In those examples where the supposed olecranon has come away the dorsal half of the articulatory surface is concave. It looks upwards and is divided from the ventral half by a convex ridge. The ventral surface looks downwards and is feebly convex dorso-ventrally and concave pre-postaxially. In no. 1 the articulation has two feebly concave surfaces, with a raised ridge for the trochlea of the distal end of the humerus. In no. 2 the dorsal half of the articulation is destroyed. The postaxial concave surface is more oblique and carried further on to the shaft of the bone, thus looking more outward than in the other specimens. This example

* H. G. Seeley, 'Ornithosauria,' 1870, pp. 45 & 46.

exhibits the raised and roughened surface for the biceps tendon in a greater degree than any of the others on this tablet.

Tablet J. *a.* 11. The seven specimens on this tablet are the proximal ends of ulnæ. No. 1 is the proximal end of a right ulna figured by Seeley, pl. ii. fig. 8 (*loc. cit.*), as the proximal end of radius. It is much smaller, but similar to *Ornithodesmus latidens*, with the central transverse ridge on the articular surface not so highly developed. This ridge and the margins of the bone on the postaxial side are worn away. The strong longitudinal ridge on the centre of the ventral surface of the shaft is also destroyed, but its base is well seen. A pneumatic foramen occurs, covered by a small daub of matrix, near the articular surface, ventral side, as in *Ornithodesmus latidens*.

Nos. 2, 3, 4, 5, 6 all have the median vertical ridge on the anterior surface of the shaft. All are close to no. 1, and thus near to *Ornithodesmus*, but the ridges, processes, and articular characters are either in an incipient or degraded state. No. 5 has lost the median area of the articulation in such a manner that it appears at first sight to be a basin-shaped depression, whereas a closer examination proves that it is due to wear. The pneumatic foramen is not seen in nos. 2–6, for the same reason.

No. 7, the proximal end of the right ulna, figured by Seeley, pl. ii. fig. 7 (*loc. cit.*), is remarkably different from the other six examples on this tablet. The only articular surface preserved is on the preaxial side. It is slightly convex and looks anteriorly. The dorsal surface and postaxial border are destroyed. There is no pneumatic foramen on the portion preserved. The great peculiarity of this specimen is on the ventral surface, where the bone is concave, with an elongated and deep pit (no foramen) for the biceps tendon near the postaxial border. This is well seen in the figure. The other pits observed are not natural, but the borings of some organism.

Distal end.

Tablet J. *a.* 10, 1–10. There are eleven examples on this tablet, the eleventh probably added since 'Ornithosauria' was published. They are the distal ends of ulnæ, and not "radii." Nos. 1, 2, and 9 are similar in character, no. 2 is the best specimen and figured by Seeley, pl. iii. fig. 1 (*loc. cit.*). On the major portion of the dorsal surface, towards the preaxial side, there is the flattened surface, against which

Proximal Ends of Ulnæ.

Group A.	Group B.	Group C.	Group D.
1. Articular surface, preaxial side, feebly convex. A robust <-shaped ridge centre of postaxial side, the branches produced to dorsal and ventral borders.	1. Articular surface dorsal half concave, with a circular pit into the shaft.	1. Articular surface dorsal side produced proximally (the epiphysis of Seeley); ventral side, two slightly concave surfaces obliquely placed for trochlear jointed humerus. No pit into shaft.	1. Articular surface, preaxial side slightly convex, looking anteriorly, postaxial side unknown.
2. Pneumatic foramen ventral surface.	2. Pneumatic foramen ventral surface.	2. Pneumatic foramen ventral surface.	2. Position of pneumatic foramen unknown.
3. Robust longitudinal ridge, ventral surface near postaxial border moderate distance below articulation.	3. Longitudinal ridge as seen in Group A absent.	3. Longitudinal ridge absent as in Group B.	3. Longitudinal ridge absent as in Groups B and C.
4. Biceps tendon attached preaxial side of this ridge, postaxial to the radius.	4. A small raised surface preaxial to radius for biceps tendon.	4. As in Group B.	4. A deep elongated pit for biceps tendon; ventral surface near the postaxial border and postaxial to radius. The raised surface as in Groups B and C absent.
Examples: J. *a.* 11, 1, 2, 3, 4, 5, and 6.	Examples: J. *a.* 9, 2, 3, 4, 5, and 6.	Example: J. *a.* 9, 1.	Example: J. *a.* 11, 7.

Distal Ends of Ulnæ.

Group A.	Group B.	Group C.
1. Dorsal surface flat. Incipient longitudinal ridge preaxial side. Dorsal surface becoming gently convex proximally.	1. Dorsal surface more concave, the longitudinal ridge more developed, and the proximal dorsal surface flatter than in Group A.	1. Dorsal surface slightly concave and longitudinal ridge moderately developed.
2. Ventral surface very inflated.	2. Ventral surface flat.	2. Ventral surface very inflated.
3. Basin-shaped pit on articular surface near preaxial border.	3. As in Group A.	3. As in Groups A and B.
4. Articular facet postaxial side, prolonged on to the ventral surface.	4. As in Group A.	4. As in Groups A and B.
5. Elevated oblique flattened surface for muscle-attachment postaxial side of dorsal surface.	5. As in Group A.	5. As in Groups A and B.
6. Preaxial border angular.	6. As in Group A.	6. Preaxial border not as angular as Groups A and B.
7. Articulation very inflated.	7. Articulation preaxial side angular, caused by convergence of the flat dorsal and ventral surface.	7. Articulation preaxial side not so inflated as Group A, or as compressed and angular as Group B.
Examples: J. *a.* 10, 1, 2, 9.	Examples: J. *a.* 10, 3, 4, 7, 8, 11.	Examples: J. *a.* 10, 5, 6, 10.

the radius rested, bordered postaxially by the longitudinal ridge. The ventral surface is strongly convex. On the articulation there is clearly visible, although filled with matrix, the circular pit near the preaxial border, for the hemispherical knob of the proximal carpal, and at the postaxial edge on the ventral surface are seen the remains of the facet for articulation with the produced border of the carpal. Distally no. 2 is very much inflated.

J. *a.* 10, 3 : the distal end of left ulna. The surface for the radius is more concave and the ridge more developed than in no. 1. The dorsal surface becomes flatter proximally, while in nos. 1, 2, and 9 it is gently convex. The distal extremity of this example differs considerably from no. 1 ; instead of being strongly inflated, both dorsal and ventral surfaces are flat, converging and forming an angle on the preaxial border. Nos. 4, 7, 8, and 11 are examples of this type. J. *a.* 10, 6, the distal end of left ulna, has a very inflated convex ventral surface, continued to the articulation. The longitudinal ridge is moderately developed. The dorsal articular surface for the radius is slightly concave. The preaxial side of the articulation is not as inflated as no. 1 nor as compressed and angular as no. 3. Nos. 5 and 10 are examples of this type.

No pneumatic foramina are to be found on any of these specimens.

Conclusions as to the Extremities of Ulnæ (see pp. 552–553).

By a comparison of the articulatory surfaces of J. *a.* 11, 1, 2, 3, 4, 5, and 6, it is quite possible that they belong to species with the same type of the distal end of humerus as nos. 21 and 32 on tablet J. *a.* 6, and therefore of Group A. Granting that the proximal ends, J. *a.* 9, 2, 3, 4, 5, and 6, Group B, have lost no epiphysis, and are as they were in life, we consider them to belong to the same reptiles, possessing the type of humerus exemplified in the distal end of humerus J. *a.* 6, 20, Group B, and thus, if our conclusions are correct, to *Ornithostoma*.

The only distal ends of humeri that J. *a.* 9, 1, Group C, could in any way articulate with are those of the Group C, of which the humerus J. *a.* 6, 30 is the type. The proximal end of the ulna J. *a.* 11, 7 must for the present remain an isolated bone, necessitating the formation of Group D, of which it is the only example.

There is no evidence available to enable the apportionment of any of the distal ends to either of the genera formed by

the premaxillæ. Group A certainly approaches *Ornithodesmus latidens*, but differs considerably in the great inflation of the ventral surface, the depth of the preaxial border, the lack of any drawing in of its distal termination into a tubercle, and no prolongation of the dorsal surface of the bone over the preaxial border as a wing. The longitudinal ridge on the dorsal surface is not as highly developed. The ventral surface of *Ornithodesmus latidens* is deeply concave, especially towards the postaxial border, before the rise of the bone for the articular facet, where, in the Cambridge specimen, the convexity is the greatest, and the articular facet on the postaxial side is more oblique.

The Carpals.

It is impossible to assign any of these bones to any given genus, but two which have been figured by Seeley in 'Ornithosauria' are sufficiently close to *Ornithodesmus latidens* to favour an assumption that they belong to a genus with the humerus of the type of Group A. These bones are J. *b.* 1, no. 7, pl. v. fig. 3, a proximal belonging to the right carpus, and J. *b.* 3, 24, pl. v. fig. 7, to the right distal carpal.

The Wing Metacarpal.

As with the other bones, only fragments of the wing metacarpal occur, and therefore comparisons with other genera from the length cannot be made. The best-preserved proximal end is J. *b.* 5, 3, figured by Seeley (pl. vi. figs. 2 & 3). It appears to belong to an entirely different family from *Ornithodesmus*.

Several specimens possess the facet, below the main proximal articulation, for the bending of the wing; but they are not as developed or directed outwards in as great a degree as in *Ornithodesmus latidens*.

The Sternum.

The anterior projecting process is the only part of the sternum preserved. It was directed well forward, downward, and oblique to the sternal plate, and not vertical as in *Ornithodesmus latidens*. They are all close to *Ornithostoma* (*Pteranodon*) and *Nyctosaurus*, but they cannot be apportioned either to the dentigerous or edentulous forms of the Cambridge Greensand for certainty.

Os innominatum.

Examples of the ossa innominata are arranged on tablet J. *b.* 10, and numbered 1–9. In those specimens, where the acetabulum is preserved, it is imperforate, and the surrounding bones anchylosed and apparently near to *Ornithostoma* (*Pteranodon*) *ingens*, where the bones are conjoined and the acetabulum shallow and imperforate.

Femur.

There is only one perfect specimen of the femur, the other examples are fragments. They may be divided into two groups :—

(1) Neck and head oblique to the shaft. Great trochanter weak. Shaft straight and large. Example : J. *c.* 2, 11, 20.
(2) Neck and head very oblique. Great trochanter robust. Shaft straight and small. Example : J. *b.* 11, 1.

Both are illustrated in 'Ornithosauria,' pl. viii. figs. 5, 6, 7, and 8. In neither group are the head and neck as terminal as in *Ornithodesmus latidens*. The shaft is not curved as much as in the American forms; otherwise the description by Professor Williston * of the femur of *Ornithostoma* (*Pteranodon*) *ingens* is near to Group 1 and also to *Nyctosaurus* (*Nyctodactylus*) †. To which genus the specimens included in Group 2 belong must remain an open question.

In concluding our examination of the Cambridge Greensand material in the Cambridge Museum, Cambridge, we find that the jaws divide into five genera—*Ornithocheirus*, *Lonchodectes*, *Amblydectes*, *Criorhynchus*, and *Ornithostoma*.

On the evidence of the premaxillæ *Ornithodesmus* is entirely separated from either genera of the Cambridge Greensand, but the fragments of the humeri and ulnæ of Group A must undoubtedly be incorporated into the same family, and there is nothing to prove that the humeri and ulnæ included in Group A should be assigned to reptiles possessing premaxillæ typical of one of the five genera. Neither can any of the other bones of the axial skeleton be

* S. W. Williston, Kansas Univ. Quart. 1893–4, ii. p. 80.
† *Id.* Field Col. Mus. Pub. 78, geo. ser. 1903, vol. ii. no. 3, p. 150.

apportioned to any particular genus, except those which, by comparison with the American forms, belong to *Ornithostoma*.

The other groups must remain isolated until some further discovery determines their relationship.

Classification.

Family **Ornithocheiridæ**.

Subfamily *Ornithocheirinæ*.

Genera Ornithocheirus (Seeley).
Lonchodectes.

Subfamily *Criorhynchinæ*.

Genera Criorhynchus (Owen).
Amblydectes.

Family **Ornithostomatidæ**.

Genus Ornithostoma (Seeley).
(*Pteranodon*, Marsh.)

In conclusion, I would like to bear witness to the magnificent work of Seeley in the determination and interpretation of such fragmentary material. It must have been a most difficult task. I also desire to thank Professor T. McKenny Hughes for his courtesy and kindness in lending me the type-specimens for study.

EXPLANATION OF PLATE XXII.

Fig. 1. Left lateral view of Cambridge specimen J. *c.* 9. *O.*, orbit; *Su.OC.CR.*, supra-occipital crest; *OC.*, occiput. × about $\frac{3}{4}$.

Fig. 2. Occiput of same specimen above the foramen magnum. *f.m.*, foramen magnum; *p.t.f.*, post-temporal fossæ. × about $\frac{1}{2}$.

Fig. 3. Posterior view of skull of same specimen. *Su.OC.CR.*, section of supra-occipital crest; *OC.*, occiput. × about $\frac{5}{8}$.

Fig. 4. Left lateral view of the tip of the upper jaw of *Criorhynchus simus* (after Owen). Nat. size.

Fig. 5. Left lateral view of a portion of the upper jaw of *Coloborhynchus clavirostris* (after Owen). The dotted lines indicate the amount of the upper jaw worn away by attrition. Nat. size.